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James A. Doyle and Peter K. Endress

4.1 Introduction

The origin of the angiosperm flower and its subsequent evolution have been major topics of discussion and controversy for over a century. Because so many of the distinctive synapomorphies of angiosperms involve the flower, its origin and the homologies of its parts are closely tied to the vexed problem of the origin of angiosperms as a group. From a phylogenetic point of view, the origin of angiosperms involves two related problems: identification of the closest outgroups of angiosperms, which may clarify homologies of their distinctive features with structures seen in other plants, and rooting of the angiosperm phylogenetic tree and identification of its earliest branches, which may allow reconstruction of the flower in the most recent common ancestor of living angiosperms. It is this second topic that we address in this chapter (for the first study, see Frohlich and Chase, 2007; Doyle, 2008). This task has become much easier in the past ten years, thanks to molecular phylogenetics.

Ideas on the ancestral flower have varied greatly since early in the last century. Two extremes were euanthial theories, which postulated that the flower was a simple strobilus that was originally bisexual and had many free parts (Arber and Parkin, 1907), and pseudanthial theories, which assumed that the first angiosperms had unisexual flowers with few parts, as in 'Amentiferae' (now

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mostly Fagales), which were later grouped to form bisexual flowers (Wettstein, 1907; review in Friis and Endress, 1990). Later variations on the pseudanthial theory proposed that the angiosperms were polyphyletic (Meeuse, 1965, 1975), while recognition of chloranthoid pollen, leaves and flowers in the Early Cretaceous fossil record (Muller, 1981; Upchurch, 1984; Walker and Walker, 1984; Friis et al., 1986; Pedersen et al., 1991; Eklund et al., 2004) contributed to suggestions that Chloranthaceae, which combine putatively primitive wood and monosulcate pollen with extremely simple flowers, often consisting of just one stamen or one carpel, might provide another model for the ancestral flower (Endress, 1986b; Taylor and Hickey, 1992).

The advent of cladistic methods raised hopes of resolving these problems. Cladistic analysis of morphological characters provided a relatively objective method for constructing trees based on as many characters as possible, on which the evolution of individual characters could be traced by using parsimony optimization. However, although morphological cladistic analyses eliminated some alternatives, such as polyphyly of the angiosperms, their implications for rooting of the angiosperms and characters of the first flower were still highly varied. Depending on assumptions on outgroups and character analysis, some studies rooted angiosperms among groups with showy flowers, placing Magnoliales (Donoghue and Doyle, 1989), Calycanthaceae (Loconte and Stevenson, 1991) or Nymphaeales (Doyle, 1996) as the sister group of all other angiosperms, but others rooted them among groups such as Chloranthaceae and/or Piperales with simple flowers (Taylor and Hickey, 1992; Nixon et al., 1994; Hickey and Taylor, 1996).

This picture was clarified dramatically by molecular phylogenetics, which used the vastly greater numbers of characters in nucleotide sequences to generate independent estimates of relationships at the base of angiosperms. The first large molecular studies, on nuclear rRNA (Hamby and Zimmer, 1992) and the chloroplast gene *rbc*L (Chase et al., 1993), suggested that molecular data might also be inconclusive, since the two analyses differed in rooting angiosperms near Nymphaeales and the aquatic genus *Ceratophyllum*, which have multiparted bisexual flowers and extremely simple unisexual flowers, respectively. However, this situation improved with analyses of other genes and concatenated sequences of several genes (Mathews and Donoghue, 1999; Parkinson et al., 1999; Qiu et al., 1999, 2006; Soltis et al., 1999, 2000, 2005; Antonov et al., 2000; Barkman et al., 2000; Zanis et al., 2002). Despite variations in outgroup relationships, all of these studies rooted angiosperms among the so-called ANITA lines, namely *Amborella*, Nymphaeales and Austrobaileyales, while confirming many clades within the remaining angiosperms (*Mesangiospermae* of Cantino et al., 2007) that had been inferred from rRNA and *rbc*L. The main variations concern whether *Amborella* and Nymphaeales form two successive branches or a clade (e.g. Barkman et al., 2000; Qiu et al., 2006) and different arrangements of basal

lines in the mesangiosperms. In Doyle and Endress (2000), we evaluated conflicts between morphological and molecular results by combining a morphological data set with sequences of three genes (18S rDNA, *rbc*L, *atp*B), with the angiosperm tree rooted on *Amborella*. As expected from the great number of molecular characters, this combined analysis generally confirmed the molecular results (for example, Nymphaeales were in the basal grade rather than linked with monocots), but there were a few exceptions. Most notably, in Laurales the sister group of Lauraceae was Hernandiaceae rather than Monimiaceae or Monimiaceae + Hernandiaceae.

Several studies have used molecular and/or combined trees as a framework for parsimony reconstruction of the evolution of floral characters (Doyle and Endress, 2000; Ronse De Craene et al., 2003; Zanis et al., 2003; Endress and Doyle, 2009), thus avoiding the circular reasoning that plagued earlier discussions. For these purposes, it is fortunate that the ANITA groups form a series of low-diversity lines that diverge sequentially below the vast majority of angiosperms; as a result, the many character states that are shared by these lines can be interpreted as ancestral in angiosperms. To some extent this circumvents the problem of identification of angiosperm outgroups, which remains one of the most intractable problems in plant evolution. Whereas morphological analyses associated living Gnetales in various ways with angiosperms, molecular analyses appear to be converging on trees with Gnetales nested within conifers (summarized in Burleigh and Mathews, 2004; Soltis et al., 2005). Morphological analyses that constrained Gnetales to a position in conifers (Doyle, 2006, 2008) identified fossil glossopterids, *Pentoxylon*, Bennettitales and *Caytonia* as extinct outgroups of the angiosperms, but there is no consensus that any of these taxa are related to angiosperms (cf. Taylor and Taylor, 2009).

The ancestral flower reconstructed by optimizing characters on trees of living taxa is the flower in the most recent common ancestor of all living angiosperms, or the crown group node. This is not necessarily the first flower, as flowers could have originated much earlier on the stem lineage leading to angiosperms. If the flower originated earlier there is no way to reconstruct its characters without fossil evidence, except perhaps to some extent by studies of the evolution of genes involved in development (Frohlich and Chase, 2007). Numerous fossil flowers are now known from the Early Cretaceous (Friis et al., 2006), but so far they have provided no clear evidence on this question, because none have been convincingly placed on the angiosperm stem lineage (Doyle, 2008; Endress and Doyle, 2009).

In this study we explore early floral evolution using the morphological data set of Endress and Doyle (2009), with a few changes made in Doyle and Endress (2010), where we used this data set to integrate Cretaceous fossils into the tree of living angiosperms. In Endress and Doyle (2009), we examined the implications

of eight alternative trees, designed to represent the spectrum of currently viable hypotheses. These included trees with the two arrangements of *Amborella* and Nymphaeales and with two arrangements within mesangiosperms – relationships among major mesangiosperm lines are still poorly resolved, presumably because they radiated in a geologically short period of time. In one mesangiosperm arrangement (called J/M), *Ceratophyllum* was the sister group of eudicots and Chloranthaceae were sister to the magnoliid clade (*Magnoliidae* of Cantino et al., 2007: Magnoliales, Laurales, Canellales, Piperales), as in analyses of nearly complete chloroplast genomes (Jansen et al., 2007; Moore et al., 2007). In the other (D&E), an updated version of the combined tree of Doyle and Endress (2000), *Ceratophyllum* (not included in Doyle and Endress, 2000) was linked with Chloranthaceae, as indicated by morphology and some molecular analyses (Antonov et al., 2000; Duvall et al., 2006, 2008; Qiu et al., 2006), and the resulting clade was sister to the remaining mesangiosperms, as were Chloranthaceae alone in Doyle and Endress (2000). However, we moved Piperales from a position linked with monocots in Doyle and Endress (2000) into the magnoliids, as the sister group of Canellales based on accumulating molecular data (Soltis et al., 2005). Relationships within major clades in the D&E and J/M trees are the same, with Lauraceae and Hernandiaceae linked based on Doyle and Endress (2000), and with *Euptelea* moved to the base of Ranunculales (following Kim et al., 2004). New taxa were inserted in positions based on molecular data. We also considered trees with and without *Archaefructus*, an Early Cretaceous aquatic plant with reproductive axes variously interpreted as flowers with numerous stamens and carpels but no perianth (Sun et al., 1998, 2002) or as inflorescences of flowers consisting of one or two stamens or carpels (Friis et al., 2003). An analysis by Sun et al. (2002) identified *Archaefructus* as the sister group of all living angiosperms, but the seed-plant analysis of Doyle (2008) placed it within the crown group, linked with the aquatic family Hydatellaceae, which were formerly considered highly reduced monocots, but have been recently shown to be basal Nymphaeales (Saarela et al., 2007). The most important changes in Doyle and Endress (2010) were re-scoring of androecial characters in Piperales in accordance with developmental data and interpretations of Liang and Tucker (1995), Hufford (1996) and Tucker and Douglas (1996), and the phylogenetic results of Wanke et al. (2007); re-scoring of floral phyllotaxis and merism in some Laurales based on Staedler et al. (2007) and Staedler and Endress (2009); and increasing the number of states recognized in the carpel number character.

In Endress and Doyle (2009) we presented inferences on the evolution of all the floral characters in our data set, emphasizing implications for the morphology of the ancestral flower and for suggestions that the simple flowers of living and fossil aquatic taxa might be ancestral. Here we take a complementary,

more taxon-oriented approach, in which we concentrate more on evolution of the flower as a whole, working upward from the base of the tree, stressing general aspects of floral organization such as phyllotaxis and number of parts. Besides reviewing our reconstruction of the flower at the basal node of extant angiosperms, we extend this approach to several important higher nodes, such as mesangiosperms, magnoliids, monocots and eudicots, noting important trends within these clades. Instead of considering all eight trees, we concentrate on the D&E tree, where *Amborella* and Nymphaeales form two successive branches and Chloranthaceae and *Ceratophyllum* are sister to the remaining mesangiosperms. The differences among the eight trees had relatively little impact on scenarios for floral evolution, presumably because few changes occurred between the initial splitting events in mesangiosperms. Perhaps most significantly, in the D&E tree the shift from the ancestral barrel-shaped ascidiate carpel to the leaf-like plicate carpel occurred once just above the base of the mesangiosperms, after divergence of the ascidiate Chloranthaceae–*Ceratophyllum* line, but it may have occurred anywhere between one and four times with the J/M chloroplast tree. In general, evolutionary scenarios for several characters are more ambiguous with the J/M tree.

For ease of discussion and economy of space, we have combined the four characters for perianth and androecium phyllotaxis and merism recognized in Endress and Doyle (2009) and Doyle and Endress (2010) into two characters (Figs 4.1A, 4.2A), in which spiral phyllotaxis is treated as a state coordinate with the trimerous, dimerous and polymerous whorled states. Phyllotaxis and merism were kept separate in Endress and Doyle (2009) and Doyle and Endress (2010), with spiral taxa scored as unknown (inapplicable) for merism, on the grounds that the contrast between whorled and spiral phyllotaxis may be a phylogenetically informative distinction, independent of merism, that would be masked by treating spiral as a state of an unordered multistate character. Similarly, presence or absence of a perianth and number of perianth whorls (series in spiral taxa) were treated as separate characters in Endress and Doyle (2009) and Doyle and Endress (2010), on the assumption that origin or loss of a perianth is a phylogenetically significant event, independent of the number of whorls, but in Fig 4.1B we treat absence of a perianth as a state of the character for number of whorls (as in Doyle and Endress, 2000). Number of stamen whorls and presence of one versus more than one stamens were also treated as separate characters in Endress and Doyle (2009) and Doyle and Endress (2010), on the assumption that flowers with one stamen deserve special recognition and cannot be assumed to be a result of reduction from one whorl, but here one stamen is treated as a state in the character for number of stamen whorls (Fig 4.2B). It may be theoretically preferable to separate characters for the presence versus absence of structures from characters for their different forms (Sereno, 2007), and the same may be true of characters such as spiral versus

whorled phyllotaxis and merism of whorls, although this coding may introduce a risk of 'long distance' effects (Maddison, 1993) that bias toward the same ancestral state in a character when it only exists in widely separated clades. However, in practice there are only a few cases in which the two approaches give different results, as is discussed below.

Sources of data on characters and taxa, and discussion of problems in character analysis can be found in Endress and Doyle (2009) and Doyle and Endress (2010). Characters were optimized on the tree using MacClade (Maddison and Maddison, 2003).

4.2 From the base of the angiosperms to mesangiosperms

We begin by discussing inferences concerning morphology of the flower at the basal node of angiosperms and near the basal node of mesangiosperms, considering first organization of the perianth (Fig 4.1), then the androecium (Fig 4.2) and finally the gynoecium (Fig 4.3). Because the basal branch in mesangiosperms in the D&E tree is the Chloranthaceae–*Ceratophyllum* clade, whose members have extremely simple flowers, the exact point of origin of several features that characterize the rest of the mesangiosperms is ambiguous. These inferences will serve as a foundation for discussion of floral evolution in major clades within the mesangiosperms. Throughout this study, it should be recognized that such parsimony-based statements are only the most economical explanations of the data; in reality, there may have been more fluctuations along evolutionary lines, as assumed by likelihood-based methods.

Because there is an alternation of lines with spiral and whorled perianth at the base of the angiosperm tree (Fig 4.1A), the inferred ancestral perianth phyllotaxis is equivocal – either spiral or whorled and trimerous. If the ancestral state was spiral, it became whorled and trimerous either once, with a reversal in Austrobaileyales, or twice, in Nymphaeales and in mesangiosperms. If it was whorled and trimerous, it became spiral independently in *Amborella* and in Austrobaileyales. This and analyses of other characters presented below indicate that many aspects of floral organization were highly labile early in angiosperm evolution, as emphasized by Endress (1987a) and Ronse De Craene et al. (2003). In Nymphaeales (setting aside Hydatellaceae) the perianth was originally trimerous, as in Cabombaceae and *Nuphar*, but it became polymerous (specifically tetramerous) within Nymphaeaceae (*Barclaya* + Nymphaeoideae = *Nymphaea*, *Euryale* and *Victoria*). Perianth phyllotaxis remained spiral within Austrobaileyales. However, the perianth is unambiguously reconstructed as whorled and trimerous at the basal node of mesangiosperms. The same results are obtained if perianth

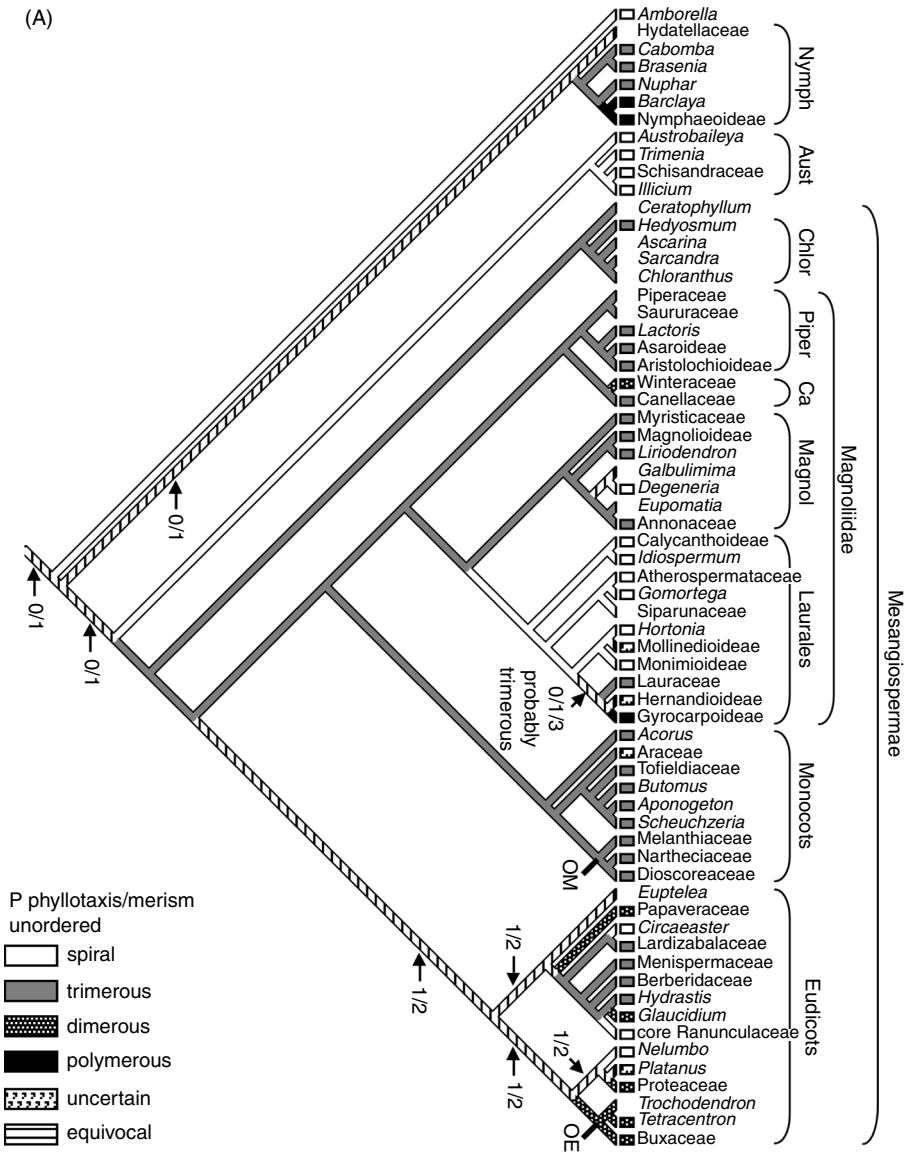

Fig 4.1 D&E tree of Endress and Doyle (2009), based on molecular and morphological data, with shading of branches showing the most parsimonious course of evolution of perianth characters (Endress and Doyle, 2009; Doyle and Endress, 2010), reconstructed with MacClade (Maddison and Maddison, 2003). (A) Character combining Endress and Doyle (2009) characters for perianth phyllotaxis (32) and merism (33). (B) Character combining Endress and Doyle (2009) characters for perianth presence (31) and number of whorls or series (34). Arrows indicate possible states on branches where the inferred character state is equivocal (e.g. in A, 0/1 = either spiral or trimerous). OM and OE indicate the probable positions of other monocots (*Petrosaviidae*) and other eudicots (*Gunneridae*, including *Pentapetalae*). Abbreviations: Nymph = Nymphaeales, Aust = Austrobaileyales, Chlor = Chloranthaceae, Piper = Piperales, Ca = Canellales, Magnol = Magnoliales.

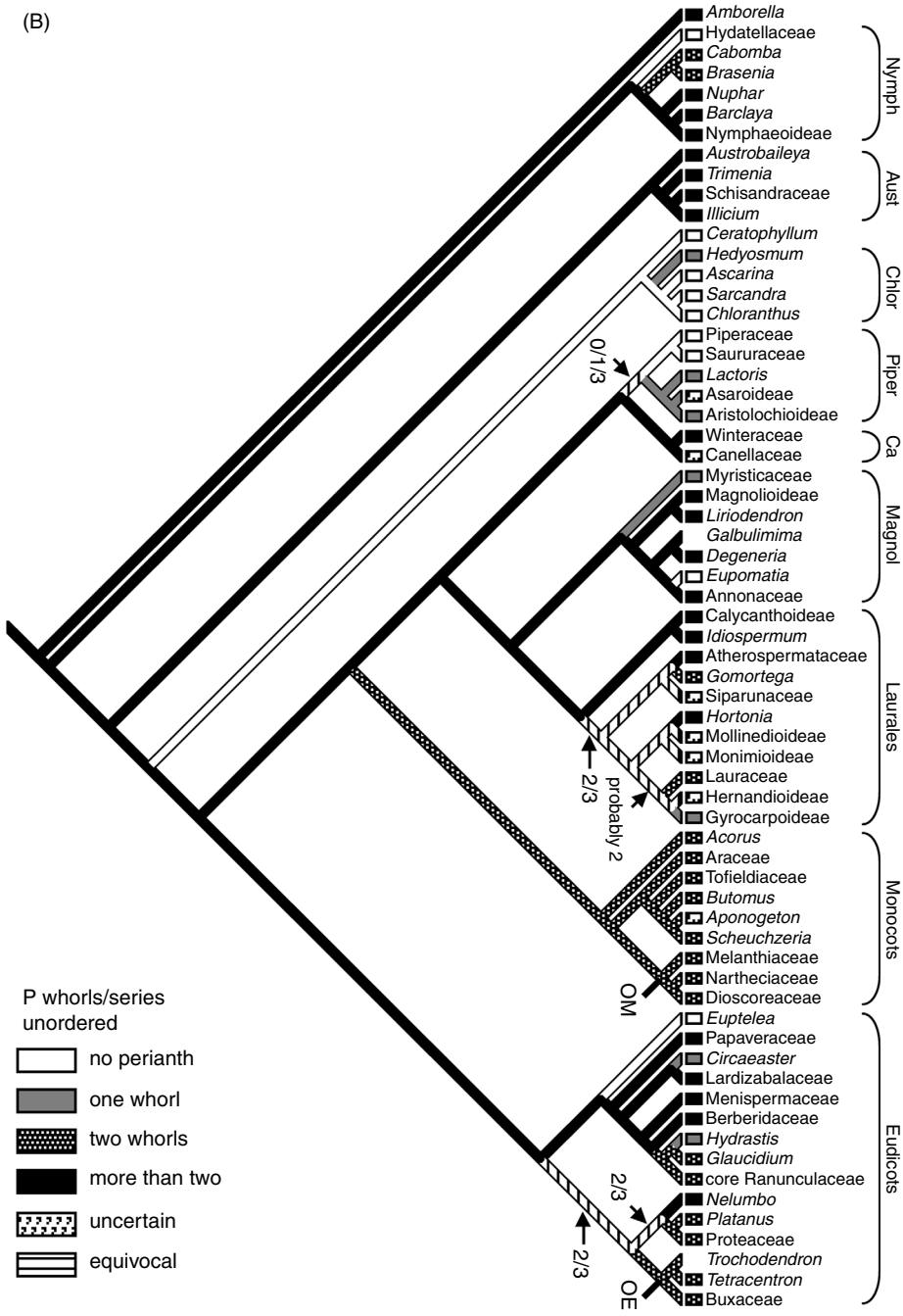
(B)
Amborella
Hydatellaceae
Cabomba
Brasenia
Nuphar
Barclaya
Nymphaeoideae
Nymph
Austrobaileya
Trimenia
Schisandraceae
Illicium
Aust
Ceratophyllum
Hedyosmum
Ascarina
Sarcandra
Chloranthus
Chlor
Piperaceae
Saururaceae
Lactoris
Asaroideae
Aristolochioideae
Piper
0/1/3
Winteraceae
Canellaceae
Ca
Myristicaceae
Magnolioideae
Liriodendron
Galbulimima
Degeneria
Eupomatia
Annonaceae
Magnol
Calycanthoideae
Idiospermum
Atherospermataceae
Gomortega
Siparunaceae
Hortonia
Mollinedioideae
Monimioideae
Lauraceae
Hernandioideae
Gyrocarpoideae
Laurales
2/3
probably 2
Acorus
Araceae
Tofieldiaceae
Butomus
Aponogeton
Scheuchzeria
Melanthiaceae
Nartheciaceae
Dioscoreaceae
Monocots
OM
Euptelea
Papaveraceae
Circaeaster
Lardizabalaceae
Menispermaceae
Berberidaceae
Hydrastis
Glaucidium
core Ranunculaceae
Eudicots
2/3
Nelumbo
Platanus
Proteaceae
Trochodendron
Tetracentron
Buxaceae
2/3
OE
P whorls/series unordered
no perianth
one whorl
two whorls
more than two
uncertain
equivocal

Fig 4.1 (cont.)

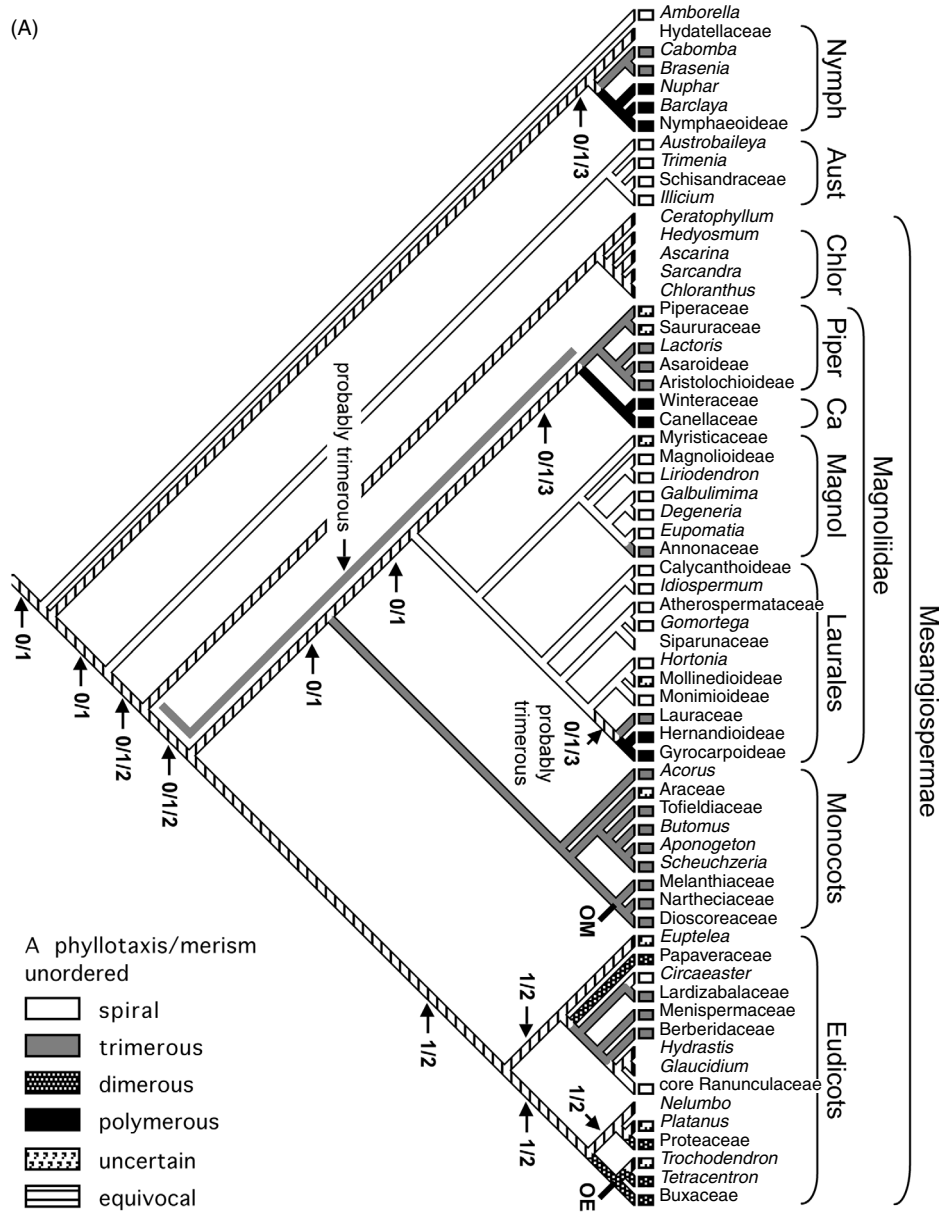

Fig 4.2 Same tree as in Fig 4.1, showing the most parsimonious course of evolution of androecium characters (Endress and Doyle, 2009; Doyle and Endress, 2010). (A) Character combining Endress and Doyle (2009) characters for androecium phyllotaxis (41) and merism (42). Grey bar indicates where use of separate characters for phyllotaxis and merism (as in Endress and Doyle, 2009) implies that the androecium was trimerous. (B) Character combining Endress and Doyle (2009) characters for one versus more stamens (40) and number of stamen whorls or series (43). Abbreviations as in Fig 4.1.

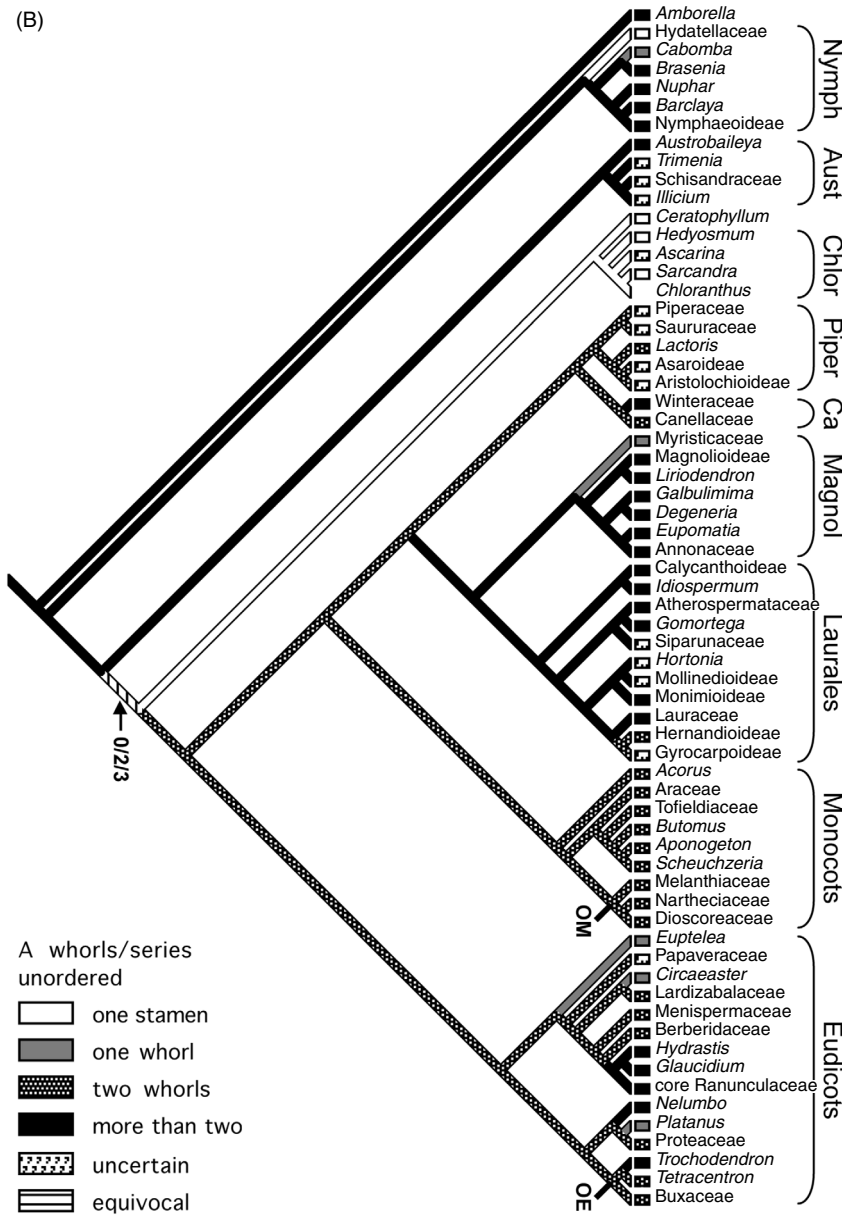
(B)
Amborella
Hydatellaceae
Cabomba
Brasenia
Nuphar
Barclaya
Nymphaeoideae
Nymph
Austrobaileya
Trimenia
Schisandraceae
Illicium
Aust
Ceratophyllum
Hedyosmum
Ascarina
Sarcandra
Chloranthus
Chlor
Piperaceae
Saururaceae
Lactoris
Asaroideae
Aristolochioideae
Piper
Winteraceae
Canellaceae
Ca
Myristicaceae
Magnolioideae
Liriodendron
Galbulimima
Degeneria
Eupomatia
Annonaceae
Magnol
Calycanthoideae
Idiospermum
Atherospermataceae
Gomortega
Siparunaceae
Hortonia
Mollinedioideae
Monimioideae
Lauraceae
Hernandioideae
Gyrocarpoideae
Laurales
Acorus
Araceae
Tofieldiaceae
Butomus
Aponogeton
Scheuchzeria
Melanthiaceae
Nartheciaceae
Dioscoreaceae
Monocots
Euptelea
Papaveraceae
Circaeaster
Lardizabalaceae
Menispermaceae
Berberidaceae
Hydrastis
Glaucidium
core Ranunculaceae
Nelumbo
Platanus
Proteaceae
Trochodendron
Tetracentron
Buxaceae
Eudicots
0/2/3
OM
OE
A whorls/series unordered
one stamen
one whorl
two whorls
more than two
uncertain
equivocal

Fig 4.2 (cont.)

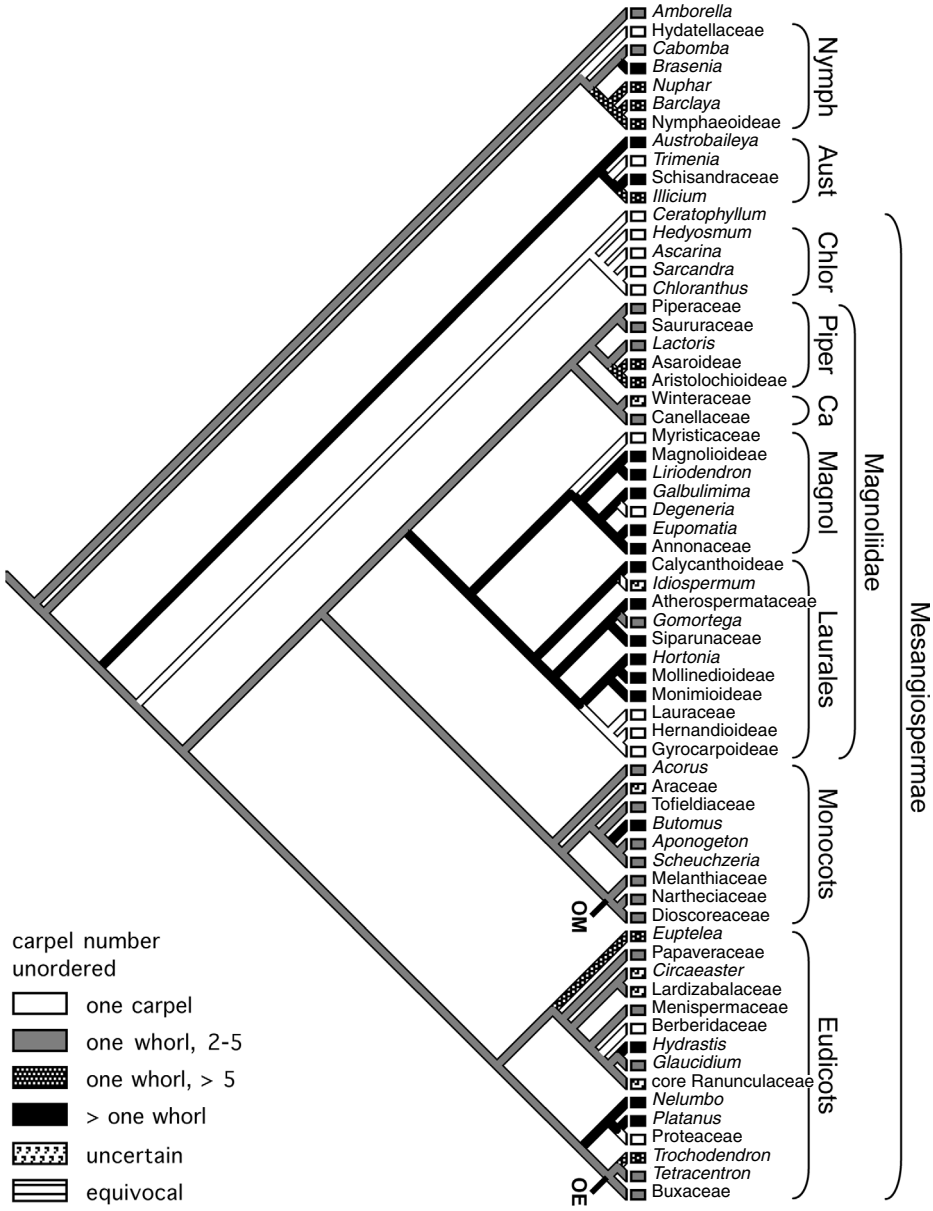

Fig 4.3 Same tree as in Fig 4.1, showing the most parsimonious course of evolution of the carpel number character (96) of Doyle and Endress (2010). Abbreviations as in Fig 4.1.

phyllotaxis and merism are treated as separate characters (Fig 4 in Endress and Doyle, 2009).

The character for number of perianth whorls (Fig 4.1B) is not strictly applicable in flowers with spiral phyllotaxis, but we have treated the number of so-called series of

tepals that roughly fill the circumference of such flowers as equivalent to the number of whorls (Endress and Doyle, 2007; Staedler et al., 2007). The ancestral state of this character is more than two whorls or series, as in *Amborella*, Nymphaeaceae and Austrobaileyales, with reduction to two whorls in Cabombaceae and complete loss of the perianth in Hydatellaceae. This state persists to the base of the mesangiosperms; because the perianth was whorled and trimerous by this point, this implies that the common ancestor of mesangiosperms had three or more whorls of three tepals. The inference that the perianth was lost in Hydatellaceae assumes that the superficially flower-like reproductive units of this group are inflorescences with basal bracts and unisexual flowers consisting of one stamen or one carpel (Endress and Doyle, 2009), rather than incompletely organized 'pre-flowers' (one possibility considered by Rudall et al., 2007) or 'non-flowers' (Rudall et al., 2009). But even if the inflorescence interpretation is incorrect, it would be most parsimonious to assume that the lack of typical floral organization in Hydatellaceae was derived rather than primitive.

The case of Chloranthaceae and *Ceratophyllum*, which are basal in mesangiosperms in the D&E tree, is more complex. In Chloranthaceae, the male flowers of *Hedyosmum* and all flowers of *Ascarina*, *Sarcandra* and *Chloranthus* lack a perianth, but female flowers of *Hedyosmum* bear three small appendages on top of the ovary of the single carpel that are usually interpreted as tepals (Endress, 1987b). Assuming that *Ceratophyllum* has a single carpel (Endress, 1994) rather than a pseudomonomerous gynoecium consisting of one fertile and one sterile carpel (Shamrov, 2009), its female flowers consist of one carpel surrounded by appendages that have been considered tepals, but are more likely bracts, since they sometimes have carpels in their axils (Aboy, 1936; Iwamoto et al., 2003). The male structures have been interpreted as flowers with tepals and numerous stamens, but they are more likely spicate inflorescences with basal bracts and male flowers consisting of one stamen (Endress, 2004), because phyllotaxis of the stamens is highly labile and their maturation is markedly delayed toward the apex (Endress, 1994), which would be anomalous for a flower, but is typical for an inflorescence. This is a case where different treatments of relevant characters give different results. In Doyle and Endress (2000), where lack of a perianth was treated as one state of the character for number of whorls and *Ceratophyllum* was not included, it was equivocal whether the perianth of *Hedyosmum* was retained from lower in the tree or secondarily derived from no perianth. In Doyle et al. (2003) and Eklund et al. (2004), where the character for presence versus absence of perianth was introduced, the presence of a perianth in *Hedyosmum* was inferred to be primitive in Chloranthaceae. However, the situation is more confused if *Ceratophyllum* is linked with Chloranthaceae. If presence versus absence of a perianth and number of whorls are treated as separate characters, as in Endress and Doyle (2009), the perianth of *Hedyosmum* may be either primitive or secondarily derived. However, when the two characters are combined (Fig 4.1B), it appears that

the perianth was lost on the line to Chloranthaceae and *Ceratophyllum*, and reappeared in *Hedyosmum*. Since there are theoretical reasons to separate presence versus absence of a structure from its different forms (Sereno, 2007), this question should be considered unresolved. In either case, as with Hydatellaceae, it would be unparsimonious to suggest that the reproductive structures of Chloranthaceae and *Ceratophyllum* are primitive.

In the ANITA lines (except *Nuphar*, which has both tepals and petals), the perianth parts are all tepals, which may be sepaloid (*Amborella*, *Trimenia*), petaloid (Cabombaceae) or differentiated into sepaloid outer organs and petaloid inner organs (Endress, 2008). With *Amborella* at the base of the angiosperms, the ancestral state is equivocal, either all sepaloid or both sepaloid and petaloid (Fig 5B in Endress and Doyle, 2009). However, the perianth can be reconstructed as sepaloid and petaloid in the common ancestor of all angiosperms except *Amborella*, and this condition persisted well into the mesangiosperms. The petaloid perianth of Cabombaceae and the sepaloid perianth of *Trimenia* were apparently derived from this state. *Nuphar* has not only sepaloid and petaloid tepals, but also inner perianth parts that fit the anatomical and developmental definition of petals (Endress and Doyle, 2009); this is clearly a convergence with the typical petals of Ranunculales in the eudicots.

Parsimony optimization indicates that the ancestral flower may have been either bisexual (the dominant traditional view) or unisexual, with both the D&E and J/M trees. This is because *Amborella* is unisexual, as are Hydatellaceae, Schisandraceae, *Ceratophyllum* and the chloranthaceous genera *Hedyosmum* and *Ascarina*. However, after the divergence of Chloranthaceae and *Ceratophyllum*, the flower in the common ancestor of the remaining mesangiosperms (magnoliids, monocots and eudicots) can be reconstructed as bisexual. As discussed in Endress and Doyle (2009), an argument in favour of the bisexual hypothesis is the fact that female flowers of *Amborella* have one or two sterile stamens – they are structurally bisexual. In any case, sex expression appears to have been remarkably labile early in the radiation of angiosperms, a conclusion supported by the mixture of unisexual and bisexual flowers in Early Cretaceous fossil floras (Friis et al., 2006).

Interestingly, the fact that *Sarcandra* and *Chloranthus* are nested among groups with unisexual flowers (*Ceratophyllum*, *Hedyosmum* and *Ascarina*) implies that their curious bisexual flowers, which consist of one carpel and either one stamen (*Sarcandra*) or a trilobed structure variously interpreted as one subdivided stamen or three fused stamens (*Chloranthus*), were derived from unisexual flowers (scenario 2 of Doyle et al., 2003). This is the only case in our data set where phylogenetic analysis implies that bisexual flowers were derived from unisexual. Cases elsewhere in angiosperms may be *Lacandonia*, nested within the otherwise unisexual monocot family Triuridaceae (Rudall and Bateman, 2006; Rudall et al.,

2009); Centrolepidaceae, if these are nested within Restionaceae (Sokoloff et al., 2009) and *Rhoiptelea*, nested within Fagales (although the occurrence of bisexual flowers in Late Cretaceous Fagales could affect this picture: Schönenberger et al., 2001). An alternative view (considered less likely by Endress, 1987b) is that the supposed bisexual flowers of *Sarcandra* and *Chloranthus* are actually pseudanthia.

As with the perianth, the ancestral state for androecium phyllotaxis (Fig 4.2A) is equivocal: either spiral or whorled and trimerous. If the ancestral androecium was spiral, it became whorled and initially either trimerous or polymerous in Nymphaeales, whereas if it was originally whorled and trimerous it became spiral in both *Amborella* and Austrobaileyales. Above this point, in constrast to the situation for the perianth, combining androecium phyllotaxis and merism has a significant effect on the results. When the two characters were kept separate (Endress and Doyle, 2009), the ancestral state in the mesangiosperms was equivocal, because Chloranthaceae and *Ceratophyllum* (both with basically one stamen) were scored as unknown, but in the common ancestor of magnoliids, monocots and eudicots the androecium was unambiguously reconstructed as whorled and trimerous. However, when the two characters are combined (Fig 4.2A), the situation becomes more ambiguous: the state both at the base of the mesangiosperms and after divergence of the Chloranthaceae–*Ceratophyllum* line, in the common ancestor of magnoliids, monocots and eudicots, may be either spiral, trimerous or even dimerous (as in many basal eudicots). This is because treating phyllotaxis and merism as an unordered multistate character obscures the fact that androecia that are trimerous (monocots, Piperales), polymerous (Canellales) and dimerous (eudicots) are all similar in being whorled. Because this is a potentially serious loss of information, it seems most likely that the ancestral state in the magnoliid–monocot–eudicot clade was whorled and trimerous, as inferred when phyllotaxis and merism were kept separate. However, this issue is not settled, because with the J/M tree the androecium may be either spiral or trimerous from the base of the mesangiosperms up to the magnoliids, independent of whether the two characters are kept separate or combined.

The scenario for number of stamen whorls (series) is less ambiguous (Fig 4.2B). The ancestral state was more than two whorls or series of stamens, which were reduced to one stamen in Chloranthaceae and *Ceratophyllum* and two whorls or series of stamens in the common ancestor of other mesangiosperms. Within Nymphaeales, the androecium was reduced to one stamen in Hydatellaceae and one whorl of six stamens in double positions in *Cabomba*. The same scenario was inferred in Endress and Doyle (2009), where the contrast between one and more than one stamen and the number of stamen whorls (series) were treated as two separate characters. Within Chloranthaceae, some *Ascarina* species have more than one stamen, but this condition was apparently secondarily

derived from one stamen, and the same is true of the three-lobed androecium of *Chloranthus*, irrespective of whether this is one subdivided stamen or three fused stamens (Endress, 1987b; Doyle et al., 2003). These results imply that the flower in the common ancestor of magnoliids, monocots and eudicots (and possibly of mesangiosperms as a whole) had three or more whorls of three tepals, but two whorls/series of stamens. Curiously, this floral diagram is not retained in any of the derivative clades, all of which undergo their own further modifications, although it may have re-appeared later within some groups (e.g. some species of *Orophea* in the Annonaceae: Buchheim, 1964; Tofieldiaceae, if the calyculus is interpreted as a perianth whorl: Remizova and Sokoloff, 2003). The closest approach is in some trimerous Ranunculales, but as discussed below, it is uncertain whether their trimerous condition is a direct retention, and they differ in having true petals.

Perhaps the most interesting characters of the stamens themselves concern overall shape and orientation of dehiscence (position of the microsporangia). A distinction is often made between laminar (leaf-like) stamens, traditionally considered primitive (e.g. Canright, 1952; Takhtajan, 1969), and filamentous stamens (with a long, narrow base), but we find it more useful to distinguish three types of stamen base (short, long and wide, long and narrow; for numerical limits see Endress and Doyle, 2009) and connective apex (extended, truncated, 'peltate'). Doyle and Endress (2000) inferred that the ancestral stamen was introrse (with adaxial microsporangia) and had a long, wide base and an extended apex, as in *Amborella*, Nymphaeoideae and (except for a truncate apex) *Illicium*. However, because Hydatellaceae, which have a typical long, narrow filament and latrose dehiscence (lateral microsporangia), have more recently been associated with Nymphaeales, the situation is now more confused (Fig 7 in Endress and Doyle, 2009). Thus, the ancestral stamen may have had either a long and wide or a long and narrow base and either introrse or latrorse dehiscence, although it does appear that the connective apex was extended. Within Nymphaeales the stamen base shows an intriguing trend from long and narrow (Hydatellaceae, Cabombaceae) through short (*Nuphar*, *Barclaya*) to long and wide (Nymphaeoideae), while it was shortened in Chloranthaceae and *Ceratophyllum*. Stamen characters at the base of mesangiosperms are highly ambiguous (an extended apex but any type of base and orientation). However, we can infer that the common ancestor of magnoliids, monocots and eudicots had a long, narrow filament. These characters are among the most homoplastic in our data set, perhaps because they are highly sensitive to changes in pollination biology.

In Endress and Doyle (2009) we recognized fewer characters for organization of the gynoecium, on the grounds that its phyllotaxis and merism are too closely correlated with those of the androecium, so treating them as independent would over-weight changes in the two sets of organs. An obvious exception is presence of

a single carpel versus more than one, a character used in Endress and Doyle (2009). In part to aid in placement of fossils, we refined this scheme in Doyle and Endress (2010) by breaking more than one carpel into three states (Fig 4.3): two to five in one whorl or series; more than five in one whorl or series (the 'star-shaped' state of von Balthazar et al., 2008), as in Nymphaeaceae and *Illicium*; more than one whorl or series, as in Schisandraceae and Magnoliaceae. With this character, the inferred ancestral state in angiosperms is one whorl or series of two to five carpels, which is retained well into the mesangiosperms. Carpels were independently multiplied by increasing their number in a single whorl/series in Nymphaeaceae (correlated with carpel fusion) and *Illicium*, and by increasing the number of whorls/series in *Brasenia* and Austrobaileyales. Reduction to one carpel occurred many times, from two to five carpels in Hydatellaceae and the Chloranthaceae–*Ceratophyllum* line, and from more than one series in *Trimenia*, as well as other times in other mesangiosperms.

As discussed in detail in Doyle and Endress (2000), Endress and Igersheim (2000) and Endress and Doyle (2009), the molecular rooting implies that the carpel was originally ascidiate, growing up as a tube from a ring-shaped primordium and sealed by secretion. This is in sharp contrast to older views that it was originally plicate (conduplicate), like a leaf folded down the middle and fused along its margins (Bailey and Swamy, 1951). If the D&E tree is correct, origin of the plicate carpel and sealing of its margins by postgenital fusion occurred in the mesangiosperms after divergence of the Chloranthaceae–*Ceratophyllum* line, in the common ancestor of magnoliids, monocots and eudicots, with several reversals (in which carpel form and sealing were less closely correlated) within these groups (Fig 4.4) and partial convergences in Nymphaeaceae and *Illicium* (Endress and Doyle, 2009). A related ancestral feature is formation of an extragynoecial compitum, where pollen tubes from one stigma can grow to ovules in another carpel through surface secretion (Endress and Igersheim, 2000; Williams, 2009). This was lost in the magnoliid–monocot–eudicot clade, but it re-appeared once or twice in Magnoliales and Laurales. Parsimony optimization indicates that the ancestral carpel contained one pendent ovule, a condition retained in *Amborella*, Hydatellaceae, *Trimenia*, *Ceratophyllum* and Chloranthaceae, which may be significant in the search for homologues of the carpel in fossil seed-plants (Doyle, 2008). The number of ovules increased several times: in Nymphaeales other than Hydatellaceae, *Austrobaileya*, Schisandraceae and one or more lines in the mesangiosperms. Among basal groups, carpel fusion occurred in Nymphaeaceae, followed by formation of an inferior ovary in *Barclaya* and Nymphaeoideae.

These results are summarized in Fig 4.4, which shows the D&E tree with the carpel form character and reconstructed floral diagrams for key nodes, assuming that the ancestral flower was bisexual. At the base are two equally parsimonious

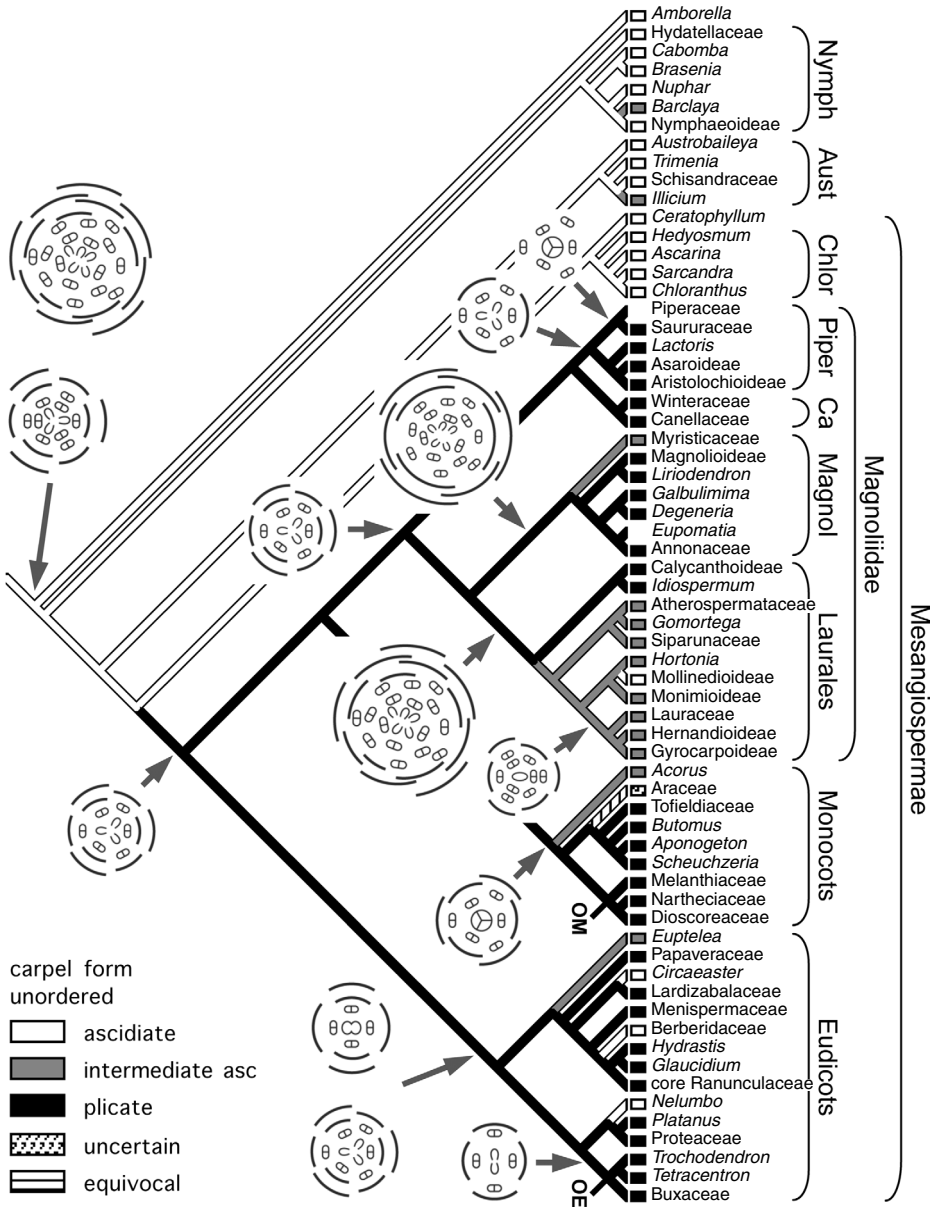

Fig 4.4 Same tree as in Fig 4.1, showing the most parsimonious course of evolution of the carpel form character (75) of Endress and Doyle (2009), with reconstructed floral diagrams for key nodes. Abbreviations as in Fig 4.1.

floral diagrams for the first angiosperms, with either spiral tepals and stamens in more than two series each, or more than two whorls of three tepals and stamens (combinations of spiral and whorled parts are also theoretically possible, but perhaps less plausible). Interestingly, there are no unequivocal changes in floral organization along the 'backbone' from the basal node to within the mesangiosperms, which may reflect both the fairly consistent floral morphology of most ANITA groups and homoplasy in the characters that do vary among them. If the ancestral flower had spiral parts, there was a shift from spiral to whorled phyllotaxis, but its location is uncertain; if the ancestral flower was trimerous, there may have been no change until reduction in the number of stamen whorls in the mesangiosperms, either before or after divergence of Chloranthaceae and *Ceratophyllum*. The reconstructed ancestral flower in the remaining mesangiosperms is trimerous, with more than two whorls of tepals, but only two whorls of stamens; as noted above, this precise architecture is not retained in any of the derived groups. Considering characters of individual floral parts, the only unequivocal change below the mesangiosperms is loss of curved hairs on the carpel before the divergence of Austrobaileyales, followed by the shift from ascidiate to plicate carpels and postgenital fusion of the carpel margins after divergence of Chloranthaceae and *Ceratophyllum*.

4.2.1 Magnoliidae

The magnoliid clade (*Magnoliidae* of Cantino et al., 2007), which consists of the APG II (2003) orders Magnoliales, Laurales, Canellales (including Winteraceae) and Piperales, includes many of the taxa that were thought to be primitive before recognition of the ANITA rooting (e.g. Takhtajan, 1966, 1969, 1980; Cronquist, 1968, 1981; Thorne, 1974). This monophyletic group should not be confused with Magnoliidae in the older sense of Takhtajan (1966, 1969, 1980) and Cronquist (1968, 1981), which was a paraphyletic grade taxon that included not only Magnoliidae in the present sense, but also the ANITA lines, Chloranthaceae and *Ceratophyllum* (as well as basal eudicot groups such as Ranunculales, removed by Takhtajan, 1969, 1980). Magnoliids are located well above the base of the angiosperm tree, but in addition to non-floral features such as monosulcate pollen and pinnately veined leaves (Doyle, 2005, 2007) some of their supposedly ancestral floral features, such as more than two whorls or series of tepals (Fig 4.1B), may have indeed been retained from the first crown group angiosperms.

Based on our data set and the D&E topology, the only unequivocal changes in floral morphology (either general organization or characters of individual organs) between the base of mesangiosperms and the base of magnoliids were the shift to plicate carpels and carpel sealing by postgenital fusion after divergence of the Chloranthaceae–*Ceratophyllum* line. The reconstructed flower in the common ancestor of magnoliids (Fig 4.4) therefore has the same floral diagram as the

common ancestor of magnoliids, monocots and eudicots: more than two whorls of three tepals, sepaloid below and petaloid above; two whorls or series of stamens with a long, narrow filament and two to five plicate carpels sealed by postgenital fusion.

Besides several whorls or series of tepals, many members of the clade consisting of Magnoliales and Laurales have other floral features that have been traditionally interpreted as primitive, but are here inferred to be derived, such as spiral perianth phyllotaxis and more than two series of spiral stamens. Given the uncertainty over the ancestral floral phyllotaxis (Figs 4.1A, 4.2A), if these cases of spiral phyllotaxis are derived, it is unclear whether they are reversals to the original angiosperm state or convergences with parallel shifts from whorled to spiral phyllotaxis in the ANITA grade, specifically in *Amborella* and Austrobaileyales. Intriguingly, phyllotactic patterns in the perianth and the androecium have been closely correlated in the groups seen so far, but this correlation breaks down in Magnoliales and Laurales (Endress and Doyle, 2007).

The first inferred change is a shift to spirally arranged stamens in more than two series in the common ancestor of Magnoliales and Laurales (Figs 4.2A, 4.2B). Under both the character definition scheme of Endress and Doyle (2009) and that shown in Fig 4.2B, the increase in number of whorls/series is a reversal to the ancestral angiosperm condition, seen in the ANITA grade, not a direct retention of the ancestral state. The status of spiral stamen phyllotaxis is more ambiguous. With the character in Fig 4.2A, where androecium phyllotaxis and merism are combined, spiral may be either secondarily derived or a retention from the first angiosperms, but under the arguably preferable scheme of Endress and Doyle (2009), where the two characters were kept separate, it is clearly derived, either as a reversal to the original condition in angiosperms (if spiral was ancestral) or a convergence with *Amborella* and Austrobaileyales (if trimerous was ancestral). However, as noted above, the scenario is also ambiguous with the J/M chloroplast tree when phyllotaxis and merism are kept separate, where spiral stamens may have extended from the first angiosperms into mesangiosperms.

Laurales show an additional shift from whorled and trimerous to spiral phyllotaxis of the perianth (Fig 4.1A), which is either a reversal to the original angiosperm condition or a convergence with *Amborella* and Austrobaileyales. With the data set of Endress and Doyle (2009), it was equivocal whether a spiral perianth originated once at the base of Laurales or more than once within the order, but with the changes in scoring of some taxa in Laurales by Doyle and Endress (2010), based on Staedler et al. (2007) and Staedler and Endress (2009), it is now an unequivocal synapomorphy of the order (Fig 4.1A). This shift coincides with origin of a hypanthium (floral cup), a conspicuous synapomorphy of Laurales. Inner staminodes are another derived feature that occurred at the base of Laurales, but as discussed below it is unclear whether this is a synapomorphy of Laurales or of

both Laurales and Magnoliales. The reconstructed ancestral flower for Laurales would be generally similar to that of living Calycanthaceae.

The peculiar stamens of most Laurales, with two basal glands and anther dehiscence by upward-opening flaps, may have originated after divergence of Calycanthaceae, but this is equivocal, because Siparunaceae and Mollinedioideae lack glands (possibly as a consequence of packing in the hypanthium) and typical lauralean flaps are absent in Monimiaceae. A partial reversal from plicate to intermediate ascidiate (and uniovulate) carpels also occurred above Calycanthaceae. A marked departure from spiral phyllotaxis and numerous series of parts occurred in Lauraceae and Hernandiaceae, with two trimerous whorls of tepals and more than two trimerous whorls of stamens in Lauraceae, and with one to three whorls of two, three or more tepals and usually two polymerous whorls of stamens in Hernandiaceae. In Figs 4.1A and 4.2A, where spiral phyllotaxis and the three different whorled conditions are states of one character, it is equivocal whether the change from spiral to whorled phyllotaxis occurred once, in the common ancestor of the two families, or independently in both of them. However, a single shift is favoured when phyllotaxis and merism are treated as separate characters (Endress and Doyle, 2009), and this scenario is further supported by the mid-Cretaceous fossil *Mauldinia* (Drinnan et al., 1990), which had a typical lauraceous floral diagram. In our analysis of the phylogenetic positions of fossils (Doyle and Endress, 2010), *Mauldinia* was attached to the stem lineage of both Lauraceae and Hernandiaceae, implying that their common ancestor had similar flowers. Other changes at this point are reduction to the characteristic single carpel of the two families and adnation of the hypanthium to produce an inferior ovary; the basal lines in Lauraceae have an inferior ovary, implying that the superior ovary of most Lauraceae is a reversal (Rohwer and Rudolph, 2005).

Decoupling of perianth and androecium phyllotaxis is most obvious in Magnoliales, where the reconstructed ancestor had more than two whorls of three tepals, but numerous spiral stamens, as in most Magnoliaceae. Correlation between the two sets of organs was restored by shifts to spiral tepals in *Degeneria* (and some derived Magnolioideae) and to whorled outer stamens in Annonaceae, becoming chaotic inwards (Endress, 1987a). Myristicaceae underwent several major modifications: a shift to unisexual flowers, reduction to one perianth whorl, reduction in number and connation of the stamens and reduction to one carpel. In the current phylogenetic context, the elongate receptacle of Magnoliaceae, often considered primitive, is instead derived. The clade consisting of *Galbulimima* (= Himantandraceae), *Degeneria*, *Eupomatia* and Annonaceae differs from Magnoliaceae in having inner staminodes (retained in the basal genus *Anaxagorea*, but lost in other Annonaceae). Since this feature also occurs in most Laurales, but not in Myristicaceae and Magnoliaceae, it may have originated independently within Magnoliales and in Laurales. However, the optimization of this character

is ambiguous with our data set, because we scored Myristicaceae as unknown, on the grounds that the absence of inner staminodes could be a side-effect of the shift to unisexual flowers, reduction in stamen number and union of stamens. As a result, it is equally parsimonious to assume that inner staminodes arose in the common ancestor of Magnoliales and Laurales, and were lost in Magnoliaceae. The fact that the staminodes of Magnoliales have distinctive food bodies might be taken as evidence for an independent origin. *Galbulimima* and *Eupomatia* show bizarre and independent departures from the basic floral type, linked with loss of the perianth and modification of the inner staminodes (and outer staminodes in *Galbulimima*) into petaloid organs, as discussed in Endress (1984, 2003) and Kim et al. (2005).

Another supposed primitive feature of many Magnoliales and Laurales is laminar stamens, partly expressed by the stamen base character (either long and wide or short, versus long and narrow). In angiosperms as a whole, it is equivocal whether the ancestral stamen base was long and wide or long and narrow, but in either case the laminar stamens of magnoliids appear to be derived: the reconstructed ancestral stamen in mesangiosperms had a long, narrow filament, which was shortened in the common ancestor of Magnoliales and Laurales, where the stamens also became more numerous and spiral (Fig 7A in Endress and Doyle, 2009). This laminar stamen was later modified again to a filamentous type in more derived Laurales. Presumably these changes are related to the well-known beetle pollination syndrome of these plants. These inferences shed light on a contrast in the orientation of dehiscence in laminar stamens in different taxa, between extrorse in Magnoliales and introrse in ANITA groups such as *Austrobaileya*. Takhtajan (1969) interpreted this difference as evidence that the ancestral stamen had lateral sporangia, which shifted to the adaxial side in some lines, but the abaxial side in others. Whereas the inferred ancestral state in angiosperms was either introrse or latrorse, and the state at the base of mesangiosperms is unresolved, magnoliids are basically extrorse, with abaxial sporangia. This is consistent with a scenario in which stamens were originally laminar and introrse, became filamentous and latrorse near the base of the mesangiosperms, shifted to extrorse at the base of the magnoliids, and then became laminar again in the Magnoliales–Laurales clade, with the sporangia now located on the abaxial side. When the stamens became filamentous again within Laurales, they shifted from extrorse to introrse, often with variation among whorls in Lauraceae.

Based on our data set, there are no unequivocal changes in floral characters on the line from the base of the mesangiosperms to the common ancestor of Canellales and Piperales. If mesangiosperms originally had a trimerous androecium, as inferred when phyllotaxis and merism are treated as separate characters, there was an increase in the number of stamens per whorl in Canellales (i.e. the androecium became polymerous), followed by connation of the stamens into

a peculiar tubular androecium in Canellaceae. In Winteraceae there was a shift from a trimerous to a dimerous perianth and an increase in the number of stamen whorls, resulting in a convergence with Magnoliales and Laurales.

Whereas Magnoliales and Laurales show floral elaboration, Piperales show a marked opposite trend for floral simplification, with reduction to one whorl of three tepals in *Lactoris* and Aristolochiaceae and complete loss of the perianth in Saururaceae and Piperaceae. With the character definitions in Fig 4.1B and in Endress and Doyle (2009), it is equivocal whether the perianth was reduced twice or in a stepwise fashion, from two whorls to one and then none. The genus *Saruma* in the Asaroideae has three petals, as well as three sepaloid tepals, which was considered a primitive feature by Thorne (1974), but given the phylogenetic position of Asaroideae, these petals are most parsimoniously interpreted as derived. In Doyle and Endress (2010) we changed the scoring of androecium merism and number of whorls in Saururaceae and Piperaceae to take into account developmental evidence that some taxa with six stamens are dimerous, with lateral stamens in double positions, rather than trimerous (Liang and Tucker, 1995; Hufford, 1996; Tucker and Douglas, 1996), and the discovery that *Verhuellia*, which has only two stamens, is basal in Piperaceae (Wanke et al., 2007; Samain et al., 2010). Nevertheless, it is still most parsimonious to reconstruct the common ancestors of both Piperales as a whole and the Saururaceae–Piperaceae clade as having two whorls of three stamens, as in the first mesangiosperms (Figs 4.2B, 4.4).

An important derived feature of many Canellales and Piperales is syncarpy, seen in Canellaceae, the bicarpellate basal genus *Takhtajania* in the Winteraceae, Aristolochiaceae (with an increase in the number of carpels) and the Saururaceae–Piperaceae clade. The type of syncarpy varies between eusyncarpous (carpels fused at the centre of the gynoecium) in Aristolochiaceae and paracarpous (carpels fused into a unilocular gynoecium with parietal placentation) in Canellaceae, *Takhtajania*, Saururaceae and Piperaceae. With apocarpous, paracarpous and eusyncarpous treated as three unordered states, optimization of this character is highly ambiguous (Fig 10B in Endress and Doyle, 2009), allowing scenarios ranging from separate origins of syncarpy in Canellaceae, *Takhtajania*, Aristolochiaceae and the Saururaceae–Piperaceae clade, to origin of paracarpous syncarpy at the base of the Canellales–Piperales clade and secondary reversals to free carpels in *Lactoris* and within Winteraceae.

4.2.2 Monocots

Assuming that the common ancestor of mesangiosperms had three or more whorls of three tepals and two whorls of three stamens, the main floral change in the origin of monocots was reduction to two whorls of tepals (Fig 4.4). This resulted in the familiar floral formula retained through monocots until the origin of highly derived groups such as Iridaceae, orchids, sedges and grasses. Another

inferred change on the monocot stem lineage was from both sepaloid and petaloid tepals to all sepaloid tepals. This condition was apparently later modified to all petaloid tepals in the common ancestor of Melanthiaceae, Nartheciaceae and Dioscoreaceae, which are the three representatives in our data set of the 'core' monocots (*Petrosaviidae* of Cantino et al., 2007).

A possibly more surprising conclusion is that the three carpels were fused into a syncarpous gynoecium in the common ancestor of monocots, and the free carpels of aquatic Alismatales, often considered primitive, are instead a reversal, as inferred by Chen et al. (2004). Remizowa et al. (2006) questioned this conclusion on the grounds that fusion of the carpels is congenital in some basal monocots (*Acorus*, Araceae, *Narthecium*), but postgenital in others (*Tofieldia*), which they suggested was evidence for multiple origins of syncarpy. However, under our organizational definition, the gynoecium of Tofieldiaceae is apocarpous with postgenital carpel connection (pseudosyncarpous in the sense of some authors) rather than syncarpous (Igersheim et al., 2001), and in any case their nested position, between syncarpous Araceae and apocarpous aquatic Alismatales, implies that their condition was derived from congenital syncarpy.

4.2.3 Eudicots

There are other major changes and problems of floral evolution in eudicots, the clade united by tricolpate (and tricolpate-derived) pollen, which includes some 75% of angiosperm species. Many members of the basal order Ranunculales have trimerous flowers (e.g. Menispermaceae, Berberidaceae), and it might be thought that these represent a retention of the trimerous state reconstructed in the perianth and probably the androecium of the common ancestor of mesangiosperms (Figs 4.1A, 4.2A, 4.4). However, Drinnan et al. (1994) suggested that eudicots originally had dimerous flowers, like most Papaveraceae, near the base of Ranunculales, and Proteaceae, *Tetracentron* and Buxaceae in the other line, which also includes the remaining or 'core' eudicots (*Gunneridae*, consisting of Gunnerales and *Pentapetalae*, Cantino et al., 2007). Often these flowers appear to be tetramerous, but a dimerous interpretation is supported by the fact that the sets of four organs arise as two successive decussate pairs and/or the stamens are seemingly opposite the perianth parts, as expected if two alternating pairs of perianth parts are followed by two pairs of stamens (Fig 4.4). The same relation of perianth parts and stamens is seen in the trimerous flowers of monocots and Ranunculales, which are also often misleadingly described as having stamens opposite the perianth parts. With a few autapomorphic exceptions, stamens in basal eudicots have a long, narrow filament, apparently retained from the base of mesangiosperms.

Our analysis indicates that the common ancestor of eudicots had more than two whorls of tepals and two whorls of stamens, as in the reconstructed common

ancestor of mesangiosperms (Figs 4.1B, 4.2B, 4.4), but their merism is equivocal: either dimerous or trimerous. In Ranunculales, if eudicots were originally dimerous, Papaveraceae retain the ancestral state, and a reversal to trimery occurred in the remaining groups; if trimery was ancestral, the dimerous condition in Papaveraceae is convergent with dimery in the other eudicot branch. Ranunculales also retain more than two whorls of perianth parts and two whorls of stamens from the common ancestor of mesangiosperms, but the inner perianth parts differ in being true petals as defined anatomically and developmentally, an important morphological innovation and a convergence with Pentapetalae. Within Ranunculales, Ranunculaceae show a shift to spiral phyllotaxis in both the perianth and androecium, with a reduction to two series of perianth parts and an increase to more than two series of stamens.

The ancestral merism is also ambiguous in the main eudicot line, as is the number of perianth whorls/series, because *Nelumbo* has more than two series of spiral tepals. However, the perianth was reduced to two whorls of tepals and became entirely sepaloid in the main eudicot clade, either once (with reversals in *Nelumbo*) or twice. Fossil evidence may help resolve some of these ambiguities. When Early Cretaceous relatives of *Platanus* are added to the analysis (Doyle and Endress, 2010), it can be inferred that both the perianth and the androecium were originally dimerous in the main eudicot line, and on the line leading to *Platanus* there was first a shift from two dimerous whorls of stamens to one whorl of five stamens (as in fossil 'platanoids'), followed by reduction to three or four stamens in *Platanus*. With or without fossil evidence, two dimerous whorls of both tepals and stamens can be reconstructed in the common ancestor of Trochodendraceae and Buxaceae, which are united by another origin of syncarpy and nectaries on the abaxial side of the carpels. Given the dramatically different flowers of *Nelumbo*, *Platanus* and Proteaceae, it may be hard to accept that they constitute a clade (Proteales), but these differences are not really a problem, because they are all a function of autapomorphies: floral gigantism and increase in the number of floral organs in *Nelumbo*, unisexuality and crowding of flowers into heads in *Platanus* and reduction of the gynoecium to one carpel in Proteaceae.

A key taxon for the question of the original merism in eudicots is *Euptelea*, which lacks a perianth. Hoot et al. (1999) suggested that *Euptelea* is fundamentally dimerous, because its floral primordium is bilateral (Endress, 1986a), but because the organs do not develop in a dimerous pattern and the shape of the primordium may be a result of space constraint by the subtending bracts (Ren et al., 2007) we scored *Euptelea* as unknown. If *Euptelea* could be shown to be basically dimerous, this would strengthen the view that dimery was ancestral in eudicots. In general, our inferences on floral evolution in eudicots are somewhat more tentative than those in other groups because we have not included other basal eudicot taxa

such as Sabiaceae (Wanntorp and Ronse De Craene, 2007) and *Didymeles* (von Balthazar et al., 2003), to say nothing of potentially relevant basal members of the remaining eudicots.

These results are of broader significance for floral evolution, because the clade that includes Trochodendraceae and Buxaceae also appears to contain the remaining eudicots, or Gunneridae, in which Gunnerales (*Gunnera*, *Myrothamnus*) have simple, apetalous flowers (clearly dimerous in *Gunnera*: Wanntorp and Ronse De Craene, 2005), whereas Pentapetalae have basically pentamerous flowers. This implies that the typical flowers of Pentapetalae, with alternating pentamerous whorls of sepals, petals and stamens, were derived from much simpler flowers with four sepaloid tepals and four stamens, whether by multiplication of whorls, incorporation of bracts into the perianth, increase in number of parts per whorl, change in identity of floral organs or some combination of these processes (cf. Soltis et al., 2003; Ronse De Craene, 2007). Wanntorp and Ronse De Craene (2005) argued that the simple flowers of *Gunnera* are reduced as an adaptation to wind pollination and therefore not significant for origin of the flowers of Pentapetalae. However, adaptive explanations and phylogenetic significance need not be mutually exclusive. As recognized by Ronse De Craene (2007), phylogenetic relationships imply that the ancestors of Pentapetalae had simple, apetalous flowers, which could have been an adaptation to wind pollination at an earlier stage that was maintained (and perhaps intensified) in Gunnerales. The resulting picture recalls scenarios for floral evolution proposed by Walker and Walker (1984) and Ehrendorfer (1989), although these were based on different sets of taxa, many of which no longer appear to be phylogenetically relevant.

4.3 Conclusions

These results can be summarized with reference to Fig 4.4, which shows reconstructed floral diagrams for key nodes. Our results indicate that the ancestral flower had more than two whorls or series of tepals and stamens, and several ascidiate carpels containing a single pendent ovule, but floral phyllotaxis appears to have been labile at first, so it is equivocal whether the floral parts were originally spiral or whorled and trimerous. Extreme floral reduction occurred in Hydatellaceae and the clade including Chloranthaceae and *Ceratophyllum*. However, a trimerous flower with more than two whorls of tepals and two whorls of stamens appears to have been established near the base of the mesangiosperms. Near this point the carpel became plicate. Within the magnoliid clade, the perianth was reduced to one whorl of tepals and lost in the Piperales, but on the line to Magnoliales and Laurales the stamens became more numerous

and spirally arranged, correlated with a strong tendency for beetle pollination, and in Laurales the perianth became spiral as well, until a reversal to trimerous whorls of both tepals and stamens, and reduction to one carpel occurred in the Lauraceae–Hernandiaceae line. Monocots lost one whorl of tepals and underwent carpel fusion, with a reversal of the latter in Alismatales. In eudicots there was a shift from trimerous to dimerous flowers, either once on the stem lineage or two or three times within the clade, followed by reduction to two pairs of tepals and stamens on the line that gave rise to pentamerous core eudicots (Pentapetalae), presumably as an adaptation to wind pollination. Cretaceous fossils have considerable potential for resolving the ambiguities in this scheme, as exemplified by the cases of *Mauldinia* in the Laurales and fossil 'platanoids' in the Proteales. It is our hope that this improved picture of patterns of early floral evolution will provide a more robust framework for process-oriented investigations of functional and developmental factors involved in the early angiosperm radiation.

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